Spatio-Temporal Analysis of *Xyleborus glabratus* (Coleoptera: Circulionidae: Scolytinae) Invasion in Eastern U.S. Forests

F. H. KOCH[1] AND W. D. SMITH[2]

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ABSTRACT The non-native redbay ambrosia beetle, *Xyleborus glabratus* Eichhoff (Coleoptera: Curculionidae: Scolytinae), has recently emerged as a significant pest of southeastern U.S. coastal forests. Specifically, a fungal symbiont (*Raffaelea* sp.) of *X. glabratus* has caused mortality of redbay (*Persea borbonia*) and sassafras (*Sassafras albidum*) trees in the region; several other Lauraceae species also seem susceptible. Although the range of *X. glabratus* continues to expand rapidly, little is known about the species' biology and behavior. In turn, there has been no broad-scale assessment of the threat it poses to eastern U.S. forests. To provide a basic information framework, we performed analyses exploiting relevant spatio-temporal data available for *X. glabratus*. First, we mapped the densities of redbay and sassafras from forest inventory data. Second, we used climate matching to delineate potential geographic limits for *X. glabratus*. Third, we used county infestation data to estimate the rate of spread and modeled spread through time, incorporating host density as a weighting factor. Our results suggest that (1) key areas with high concentrations of redbay have yet to be invaded, but some are immediately threatened; (2) climatic conditions may serve to constrain *X. glabratus* to the southeastern U.S. coastal region; and (3) if unchecked, *X. glabratus* may spread throughout the range of redbay in <40 yr. Disruption of anthropogenic, long-distance dispersal could reduce the likelihood of this outcome.

KEY WORDS *Xyleborus glabratus*, ambrosia beetle, redbay, climate matching, cost-weighted distance

The non-native redbay ambrosia beetle, *Xyleborus glabratus* Eichhoff (Coleoptera: Curculionidae: Scolytinae), has become a significant pest in southeastern U.S. coastal forests. It was first recorded in the United States in 2002, when three adults were collected from traps placed in Port Wentworth, GA, as part of an early detection effort funded by the USDA Forest Service (Rabaglia 2003, Fraedrich et al. 2007). *X. glabratus* was likely established in the vicinity by this time, but the beetle's potential impact was unclear until it was linked to severe mortality (>75% trees killed) of redbay (*Persea borbonia* L. Spreng.) on Hilton Head Island, SC, in 2003–2004 (Rabaglia 2003, Fraedrich et al. 2007). The trees actually died of laurel wilt, a disease caused by a recently identified fungal symbiont (*Raffaelea* sp.) of *X. glabratus;* the beetle is the only known vector (Fraedrich et al. 2007). By 2005, *X. glabratus* and the laurel wilt fungus were linked to redbay and, in some cases, sassafras [*Sassafras albidum* (Nutt.) Nees] mortality in several counties in Georgia and South Carolina, as well as redbay mortality at the Timucuan Ecological and Historic Preserve in Duval County, FL (Mayfield and Thomas 2006). The beetle's extent in the United States has continued to expand steadily (Fig. 1; most current distribution map is available from http://www.fs.fed.us/r8/foresthealth/laurelwilt/dist_map.shtml), with anecdotal estimates of the rate of spread ranging from ≈30 to 100 km/yr; accidental long-distance transport by humans is likely also a factor, as suggested by the detection of *X. glabratus* in Indian River County, FL, in 2006, >200 km from the closest other county known to be infested.

Xyleborus glabratus is 1 of 10 ambrosia beetle species first reported in the United States between 1985 and 2005 (Haack 2006). The species is native to India (the states of Assam and Bengal), Bangladesh, Myanmar, Japan (including the Bonin Islands), and Taiwan (Holistic Insect Systematics Laboratory 2004, Rabaglia et al. 2006). Its arrival is consistent with predictions that newly invading ambrosia beetle species would likely come from Asia and become established in the eastern United States, where environmental conditions are most compatible (Atkinson et al. 1990, Schiefer and Bright 2004). *X. glabratus* was likely introduced through solid wood packing materials (Fraedrich et al. 2007); species from the genus *Xyleborus* have historically been among the most commonly intercepted Scolytinae species in commercial cargo shipments arriving at U.S. ports of entry (Haack 2003). Notably, a substantial proportion of all Scolytinae interceptions in the last two decades have occurred in the southeastern United States (Haack 2006).

The cryptic nature of ambrosia beetles makes them difficult to detect, such that they may travel unnoticed in shipments of trees or wood products (Oliver and Mannion 2001, Rabaglia et al. 2006). Most ambrosia

[1] Corresponding author: Department of Forestry and Environmental Resources, North Carolina State University; 3041 Cornwallis Rd., Research Triangle Park, NC 27709 (e-mail: fkoch@fs.fed.us).

[2] USDA Forest Service, Southern Research Station, Research Triangle Park, NC 27709.

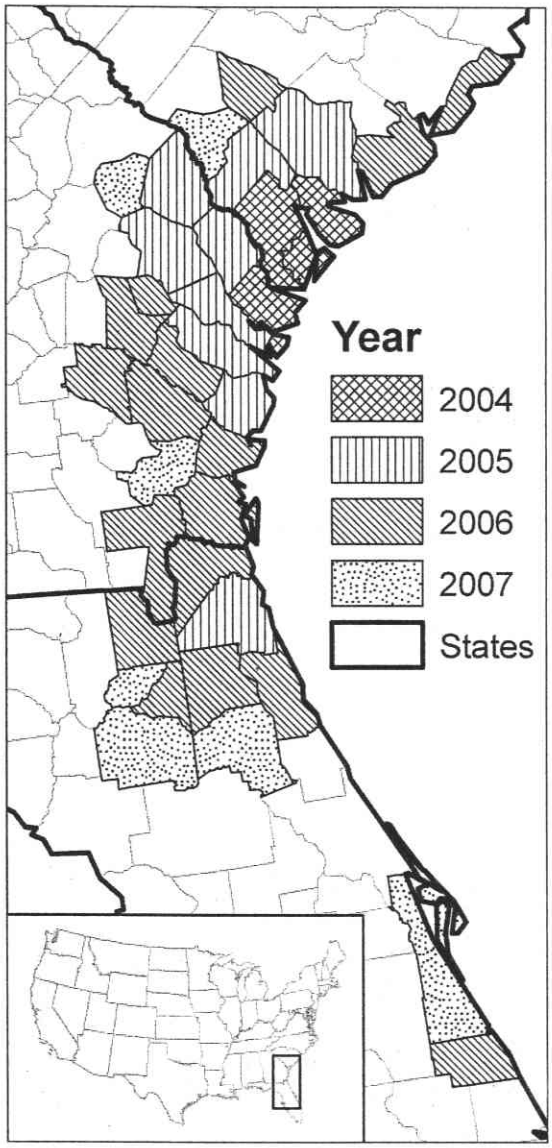

Fig. 1. County distribution of redbay mortality caused by *X. glabratus* and the associated laurel wilt fungus (*Raffaelea* sp.). Yr indicates first confirmed detection. Map is current through October 2007; the most recent version is available from the USDA Forest Service (http://www.fs.fed.us/r8/foresthealth/laurelwilt/dist map.shtml).

beetle species exhibit a fairly broad range of host plants (Beaver 1979, Rabaglia 2003, Schiefer and Bright 2004). Species from the tribe Xyleborina, in particular, have a polygamous, extreme inbred sibmating system (Normark et al. 1999, Rabaglia 2003). All of these factors combine to facilitate their spread and establishment in new areas. Despite this, ambrosia beetles are generally viewed as secondary invaders (Kühnholz et al. 2001), and *X. glabratus* is indeed believed to attack only stressed or injured trees in its native range (Rabaglia 2003). However, *X. glabratus* seems to resemble other non-native ambrosia beetle species in that, on invading the United States, it has attacked apparently healthy host trees (Oliver and Mannion 2001, Mayfield and Thomas 2006).

Whereas bark beetles feed on the phloem tissue of their hosts, ambrosia beetles feed on symbiotic fungi (i.e., ambrosia), typically carried in the mycangia of females and introduced when they bore galleries into the living sapwood of host trees or shrubs (Furniss and Carolin 1977, Kühnholz et al. 2001, Mizuno and Kajimura 2002). These fungi may be pathogenic (Kühnholz et al. 2001, Oliver and Mannion 2001), although no *Raffalea* species was previously known to kill woody plants until mass mortality of oaks (*Quercus* sp.) in Japan was attributed to *Raffalea quercivora* Kubono et Shin, a fungal symbiont of the ambrosia beetle *Platypus quercivorus* Murayama (Kubono and Ito 2002, Kinuura and Kobayashi 2006). It has been hypothesized that fungi associated with non-native ambrosia beetles may be more pathogenic in hosts with which they have not co-evolved, and this may partially explain the increased prevalence of invasives such as *X. glabratus* on apparently healthy hosts and the increased mortality of those hosts (Kühnholz et al. 2001).

Documented hosts of *X. glabratus* in the beetle's native range include one species each from the Dipterocarpaceae (*Shorea robusta* Gaertner f.), Fagaceae [*Lithocarpus edulis* (Makino) Nakai], and Fabaceae (*Leucaena glauca* L. Benth.) families, as well as three species from the Lauraceae family: *Lindera latifolia* Hook. f., *Litsea elongata* (Wall. ex Nees) Benth. and Hook. f., and *Phoebe lanceolata* (Wall. ex Nees) Nees (Rabaglia et al. 2006). All currently known hosts in the southeastern United States are Lauraceae species. Besides redbay and sassafras, the laurel wilt fungus has been found on two shrubs, pondberry [*Lindera melissifolia* (Walt.) Blume] and pondspice (*Litsea aestivalis* L. Fern.), both of which are critically endangered (Fraedrich et al. 2007, USDA Forest Service 2007b). Laboratory pathogenicity tests suggest several other Lauraceae species found in the United States are susceptible to the fungus: California bay laurel [*Umbellularia californica* (Hook. and Arn.) Nutt.], swampbay [*Persea palustris* (Raf.) Sarg.], northern spicebush (*Lindera benzoin* L. Blume), and the non-native but commercially planted avocado (*Persea americana* Mill.) (USDA Forest Service 2007b).

There are ongoing field and laboratory studies to address the many unknowns regarding the biology, behavior, and potential for control of this recently emerged pest (USDA Forest Service 2007b). Forest health managers and policymakers will also need information from broader spatial and temporal scales as they decide how best to manage the expansion of *X. glabratus* and its associated fungus. To our knowledge, there has not been a broad-scale assessment of the threat *X. glabratus* represents to eastern U.S. forests, so we made the completion of such an assessment our primary objective. In support of this objective, we performed analyses in which we could exploit the limited, coarse-scale data that are typically available for a new invasive pest. First, we mapped the densities of redbay and sassafras, the two most important host

species in the eastern United States. Second, we used climate matching to delineate potential limits to the geographic distribution of *X. glabratus* and its associated fungus. Third, we used county-level infestation data to estimate a rate of spread for *X. glabratus* and spatially modeled the pattern of spread through time, incorporating host density as a weighting factor. By combining these analyses, we hoped to describe the regional pattern of risk and provide a foundation for prioritizing future management and research efforts.

Materials and Methods

Except where specified, we used ArcGIS 9.2 software, primarily the Spatial Analyst and Geostatistical Analyst extensions (Environmental Systems Research Institute 2002, 2003), to perform geospatial operations, and SAS 9.1 (SAS Institute 2004) for statistical analyses.

Host Density Maps. We generated density maps for redbay and sassafras, the most prominent of the confirmed host species of *X. glabratus*, through ordinary kriging (Cressie 1993) of USDA Forest Service Forest Inventory and Analysis (FIA) phase 2 plot data. The FIA Program collects data from a network of permanent ground plots distributed across the United States. Each plot represents ≈2,400 ha of land area (Reams et al. 2005). The 1998 Farm Bill (Public Law 105–185) prescribed that FIA was to perform annual forest inventories; typically, 1/5 of the plots in a state (or 1/10 in Pacific Coast and Intermountain West states) are visited in a given year, yielding a complete inventory in 5 (or 10) yr (Reams et al. 2005). The cycle is repeated, allowing the estimation of forest attributes through time. A number of states in the eastern United States have already completed at least one cycle of the annualized FIA inventory. In addition, all states performed periodic forest inventories before annualization. As a result, it is possible to assemble a comprehensive, nationwide network of plots, most of which have been measured in the past 10 yr. A consistent set of quantitative and qualitative attributes are recorded for trees (>2.5 cm diameter) on each plot, allowing calculation of density, in trees per hectare, for each tree species present (USDA Forest Service 2007a). To preserve landowner privacy and field plot integrity, the plots' geographic coordinates are systematically manipulated before the release of the data to the public. However, this perturbation has been shown to have a negligible effect on the accuracy of kriging estimates (Coulston et al. 2006).

For redbay and sassafras, we first identified all of the Forest Service ecoregion sections (McNab et al. 2005) that contained FIA plots in which each species occurred (19 sections for redbay, 57 sections for sassafras). For each species, we assembled all plots that fell within the identified ecoregion sections into a geographically referenced sample (N = 24,984 plots for redbay, N = 59,844 plots for sassafras) of trees per hectare values. We fit a spherical semivariogram model to the sample for each species using weighted least squares (Cressie 1993); the fitted models subsequently determined kriging weights during spatial interpolation. To improve the likelihood that only ecologically similar plots would influence the predicted values at unknown locations, we performed separate interpolations for each ecoregion section. Predicted values were estimated based on the 30 closest FIA plots or, if the number of plots within a 60-km radius of an unknown location was <30, then based on all plots that fell within this distance threshold. The resulting kriged surfaces for each section were merged into comprehensive trees per ha maps (1-km^2 spatial resolution) for each species, which we masked using a forest cover map developed by the USDA Forest Service Remote Sensing Applications Center from Moderate Resolution Imaging Spectroradiometer (MODIS) satellite imagery.

Climate Matching. Although there are no definitive ecological rules regarding where an invasive species is likely to become established, climate strongly shapes the distribution and abundance of insect species (McKenney et al. 2003, Peacock et al. 2006). Climate matching, which falls under the broader umbrella of ecological niche modeling, is a predictive approach that assumes the potential geographic extent of a species is constrained by the same climatic conditions that limit the species' distribution within its native range (Peterson 2003). A number of software tools have been developed to generate niche models using continental- or global-scale climatic and environmental data (McKenney et al. 2003, Peterson 2003); the CLIMEX model, for instance, was designed for application to invasive pest species, including insects (Vera et al. 2002, Sutherst and Maywald 2005). We compared climatic conditions in the conterminous United States with conditions in the native range of *X. glabratus* using the North Carolina State University–APHIS Plant Pest Forecast System (NAPPFAST), a recently developed, Internet-based modeling environment (http://www.nappfast.org). NAPPFAST links global data sets for a large suite of climatic and environmental variables with biological modeling templates (Magarey et al. 2007). It includes a climate matching tool with a map-based interface for entering features (polygons or points) representing a pest species' known geographic range. Based on a user-selected set of input variables, NAPPFAST generates gridded maps (≈10-km^2 resolution) of all areas worldwide with conditions matching those in the defined range.

We used NAPPFAST to generate a climate-match map depicting the potential range of *X. glabratus* in the United States. To represent its presumed native range, we first delineated the Asian countries where the beetle is known to occur in the NAPPFAST map interface. Because specific observational data on the beetle's distribution were unavailable, we typically included entire countries in our delineations. However, we included only the states of Assam and Bengal from India. Furthermore, we omitted Hokkaido and the northern part of Honshu from our delineation of Japan; *L. edulis*, the only host of *X. glabratus* found in Japan, is limited to southern portions of the country (Levy-Yamamori and Taaffe 2004, Global Biodiversity Information Facility 2007).

Table 1. Variables used in climate matching model, including their minimum and maximum values found within the estimated native geographic range of *X. glabratus*

Variable	Minimum value	Maximum value
10-yr mean extreme min. cold temp (°C)	−26.67	15.56
30-yr mean growing degree days (baseline temp 10°C)[a]	1,645	13,036
30-yr mean growing season moisture (%)[b]	61	482
30-yr mean April precipitation (mm)	2.03	301.5
30-yr mean May precipitation (mm)	44.45	632.21
30-yr mean June precipitation (mm)	80.01	949.45
30-yr mean July precipitation (mm)	139.45	918.21
30-yr mean Aug. precipitation (mm)	105.41	916.18
30-yr mean Sept. precipitation (mm)	95.5	579.12
30-yr mean Oct. precipitation (mm)	46.48	300.48

[a] The contribution of any given day in the year to the cumulative annual growing degree-days is based on the difference between the mean of the minimum and maximum daily temperature and the baseline temperature.

[b] Percent ratio of precipitation to potential evapotranspiration (see Akin 1991).

In general, temperature is the most important climatic variable affecting the distributions of insect species, but species' distributions are rarely determined by a single variable, e.g., moisture also affects insect life cycles and host availability (Baker et al. 2000, Peacock et al. 2006). Conversely, the ability to include predictor variables from a large suite of possibilities may be problematic, because predictive power decreases with a greater number of variables caused by the increased potential for spurious correlations (Logan et al. 2003). With these points in mind, we applied a model for the climate-match map that included three annual variables (Table 1): 10-yr extreme minimum temperature; growing degree-days, a measure of accumulated warmth supporting the growth of organisms; and growing season moisture percentage (Akin 1991), a ratio of precipitation to potential evapotranspiration that reflects the overall water budget. In addition, because seasonal variation in climatic conditions may also influence species' potential distributions, we included the amount of rainfall in each month of the approximate growing season, April through October (Table 1). For evaluation, we overlaid the results of the model on the distributions of redbay and sassafras as mapped from FIA plot data.

Spread Modeling. The rate of spread for an invasive forest pest may be reliably estimated from coarse, county-scale infestation data; indeed, such an estimate is unlikely to differ significantly from the estimate possible with a spatially dense monitoring network (Tobin et al. 2007a). We estimated a rate of spread for *X. glabratus* and its associated fungus using the county infestation data depicted in Fig. 1. We followed procedures, outlined by Banks (1994), for calculating the velocity of an expanding dispersion wave under the assumption of radial dispersion with exponential population growth. We first calculated annual infestation extents for 2004, 2005, and 2006 as the total area of all counties infested by *X. glabratus* as of the year in question: 4,398 km^2 in 2004, 18,965 km^2 in 2005, and 41,480 km^2 in 2006. If the dispersion geometry is assumed to be semicircular (i.e., constrained on one side by a barrier such as a coastline), the infestation extent A at time t, and its square root—which generally increases linearly with time (Hengeveld 1989)—may be approximated as

$$A = \frac{\pi R^2}{2} = 2\pi a D t^2 \qquad [1]$$

and

$$\sqrt{A} = \sqrt{2\pi a D t} \qquad [2]$$

where R = the radius of the semicircular invasion extent, a = the net growth rate, and D = the dispersion coefficient (Banks 1994). We applied the 2004–2006 data in a least squares regression of t (yr) on $\sqrt{A}$ to derive an estimate of $\sqrt{2\pi a D}$ and, subsequently, the dispersion velocity, $2\sqrt{aD}$, for *X. glabratus* in kilometers per year.

Based on this estimated rate of spread, we modeled the range expansion of *X. glabratus* through time using a cost-weighted distance function in a gridded geographic information system (GIS). Cost-weighted distance functions have seen recent application for modeling habitat connectivity and the migration of organisms within those habitats (Michels et al. 2001, Adriaensen et al. 2003, Dedecker et al. 2007). Conceptually, these functions adjust the Euclidean distance between any given cell in a map grid and a designated source cell (e.g., the location of an initial infestation) according to an underlying resistance grid, such that the effective distance, or cost of traveling, between the cells may be more or less than the Euclidean distance; resistance values greater than one increase, and values less than one decrease, the effective distance. In the output grid of a cost-weighted distance function, each cell is assigned a value representing the least cumulative cost of traveling between that cell and the nearest designated source cell (Environmental Systems Research Institute 2002). Algorithmically, for any movement from cell X_i to one of its neighbors X_{i+1}, the cumulative cost is calculated as the cost to travel from the nearest source cell to cell X_i, plus the average cost of moving through X_i and X_{i+1}, where cost equals the spatial resolution of the grid (i.e., the distance between adjacent cell centroids) multiplied by the value from the underlying resistance grid (Environmental Systems Research Institute 2002, Adriaensen et al. 2003, Dedecker et al. 2007). Averaging ensures that the relationship between cells is symmetrical (Adriaensen et al. 2003). With respect to a cell and its four diagonal neighbors, costs are multiplied by $\sqrt{2}$ to reflect the greater distance between them (Dedecker et al. 2007).

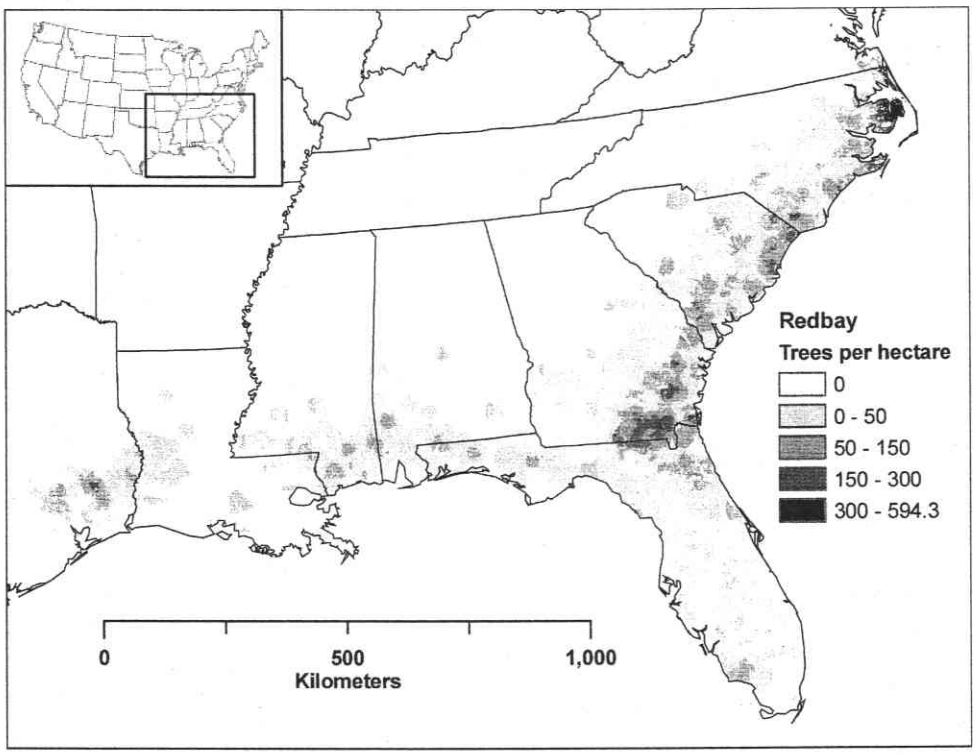

Fig. 2. Map of redbay density in trees per hectare.

Developing a resistance grid with appropriate values is the chief obstacle for cost-weighted distance analyses, often requiring detailed literature review and expert judgment (Adriaensen et al. 2003). However, in cases where little is known about a pest, it is possible to adopt simplifying assumptions and estimate resistance values from the few relevant data that are available. We developed a resistance grid for *X. glabratus* using a map of host density, under the assumption that the rate of spread for the beetle across a given region is inversely related to availability of susceptible hosts. The primary component of the host density map was our kriged map of redbay trees per hectare. Although *X. glabratus* has been observed to attack sassafras trees, these attacks have thus far occurred in areas where redbay is common; thus, it remains uncertain whether the beetle is attracted to and will infest sassafras in the absence of redbay. Therefore, we only included sassafras trees per hectare in the total host density value for grid cells where the redbay trees per hectare value was also greater than zero.

We generated a series of simple step functions, relating host density to resistance, in which we varied the minimum and maximum resistance values and the threshold values defining each step. We applied these step functions to construct preliminary resistance surfaces and subsequent spread maps, which we compared with the county infestation data. After selecting the step function that best approximated the infestation pattern through time, we developed a continuous resistance function by fitting this step function with the complemented Weibull equation (Haefner 2005), a flexible equation regularly used for biological modeling applications:

$$y = a \times \exp\left(-\left[\frac{x}{b}\right]^c\right) \qquad [3]$$

where x = the trees per hectare value, y = the cost value, a = a parameter that scales the maximum value, b = a parameter that controls the point on the x-axis at which the function is approximately zero, and c = a parameter specifying whether the function is convex or concave. We estimated parameters a, b, and c for the equation using PROC NLIN in SAS (SAS Institute 2004). We applied the resulting continuous function to our map of host density to generate our resistance grid, which we used to create a map of cost-weighted distance (1-km^2 resolution) from points of origin (i.e., source cells) in Beaufort County, SC, as well as Duval and Indian River Counties in Florida. We assumed the latter two points of origin represented initially isolated infestations caused by accidental long-distance transport of the redbay ambrosia beetle from locations to the north. We assumed all three originating infestations began 1 yr before the confirmed presence of the beetle and/or fungus at each location (i.e., 2004 for Beaufort County, SC; 2005 for Duval County, FL; 2006 for Indian River County, FL). We reclassified the output cost-weighted distance map using an increasing series of equal intervals, derived from the calculated rate of spread for *X. glabratus* (i.e., one times the

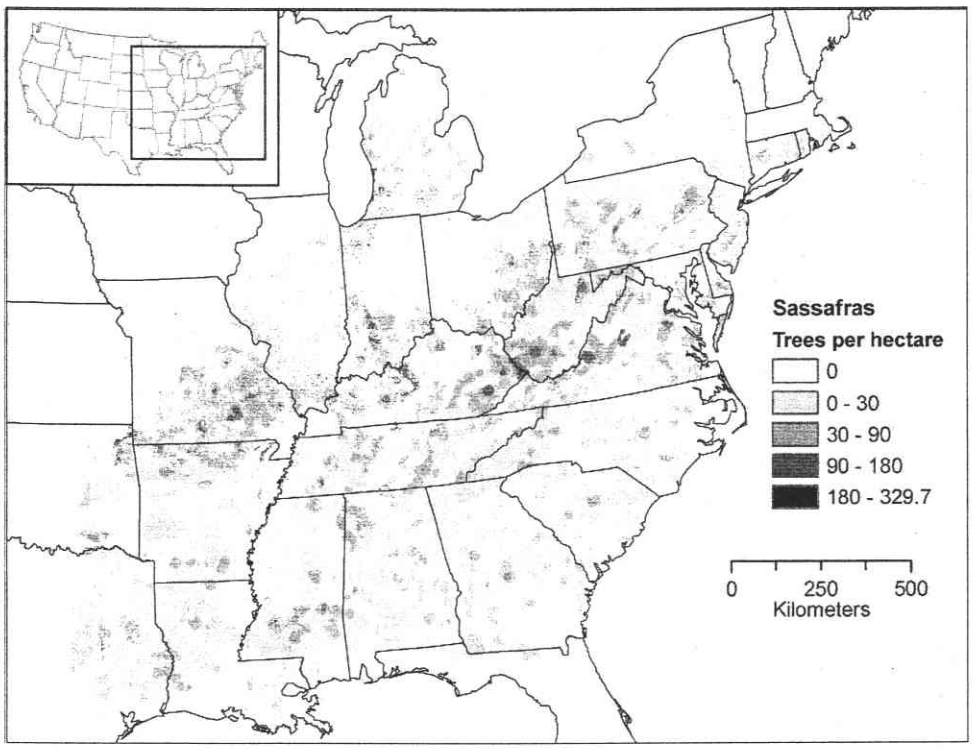

Fig. 3. Map of sassafras density in trees per hectare.

rate of spread, two times the rate of spread, etc.), to represent the area the beetle would be likely to invade with each additional year of spread.

Results

Host Density Maps. Semivariogram parameters and descriptive statistics for the spatial interpolations of redbay and sassafras density (Figs. 2 and 3) are shown in Table 2. Redbay (Fig. 2) is distributed throughout the coastal plain of the southeastern United States, typically at low densities (<50 trees/ha). Its range extends along the Atlantic Coast from southern Florida to southern Virginia and west along the Gulf of Mexico to eastern Texas. An apparent break in the distribution of redbay near the Mississippi River is primarily because of the limited amount of forestland in this area. There are several areas of moderate to high redbay density in Georgia and South Carolina, particularly a large area in southern Georgia, most of which falls just beyond the counties where *X. glabratus* is known to be present (see Fig. 1). A similar area falls just north of the known invaded counties in South Carolina. The greatest concentration of redbay by far is found on the Albemarle Peninsula of eastern North Carolina, where redbay densities are consistently >300 trees/ha. Sassafras (Fig. 3) is widely distributed at low densities (<30 trees/ha) throughout the southeastern United States, in some cases overlapping the distribution of redbay. There are a few areas of moderate to high sassafras density in Mississippi, but high concentrations of sassafras are most typically found to the north, especially in a band stretching from northeastern Oklahoma to Ohio and West Virginia. Sassafras persists at moderate densities into the lower peninsula of Michigan and can be found at low densities in New England as far north as New Hampshire. Notably, with the exception of some gaps in the Piedmont region from Georgia to Virginia, and in the sparsely forested area along the Mississippi River, the distribution of sassafras appears to be nearly continuous starting at the upper portion of the southeastern U.S. coastal plain.

Climate Matching. Each variable used in the climate matching model (Table 1) exhibited a wide range of values, which may be attributed to the approximate manner in which we defined the native geographic range for *X. glabratus* (i.e., delineating countries or large portions of countries instead of observations of the beetle's occurrence at specific point locations). Despite the coarseness of the inputs, the map resulting from the model (Fig. 4) suggests that the suitable area is largely constrained to the south-

Table 2. Parameters (nugget, sill, and range) of the semivariograms used in ordinary kriging of redbay and sassafras trees per hectare, with descriptive statistics (mean of the observations and RMSE from cross-validation)

Species	Nugget	Sill	Range	Mean	RMSE
Redbay	9,431.69	2,856.25	355,600 m	14.18	104.80
Sassafras	8,142.14	1,972.86	212,480 m	16.70	95.41

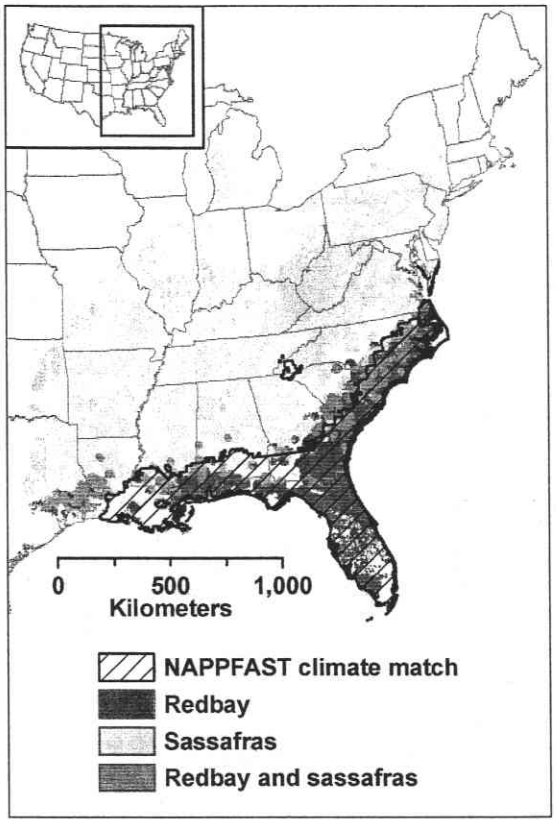

Fig. 4. Predicted U.S. range limits for *X. glabratus* based on climate matching with the species' estimated native geographic range.

eastern U.S. coastal plain, or essentially the range of redbay. With the exception of a small area in the southern Appalachian Mountains, no other part of the conterminous United States is identified as suitable under the model.

Spread Modeling. The calculated rate of spread for *X. glabratus* was 54.8 km/yr. The fitted equation for the continuous function relating host density (x), in trees per hectare, to resistance (y) was

$$y = 3.0041 \times \exp\left(-\left[\frac{x}{15.6505}\right]^{0.1927}\right). \quad [4]$$

A graph of this function (Fig. 5) indicates a maximum resistance value of three when no host is present, a resistance value of 1 (i.e., where the cost-weighted distance is equivalent to the Euclidean distance) at ≈25 trees/ha, and a resistance value of ≈0.4 at the highest possible host density (≈600 trees/ha). The function allows limited spread across areas with little or no host, which is realistic given the coarse resolution at which host presence is represented. Based on the resistance surface generated with this function, the cost-weighted distance model of *X. glabratus* spread (Fig. 6) suggests that the beetle could reach the northern and southern extents of redbay (in Virginia and Florida, respectively) between 2015 and 2020 and the western extent of redbay by 2040.

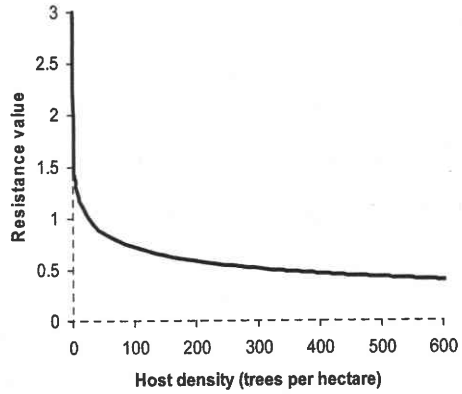

Fig. 5. Plot of the continuous function, relating resistance value to host density, used to generate the resistance surface for cost-weighted distance modeling.

Discussion

Host Density Maps. High root mean squared error (RMSE) values from cross-validation when compared with the observed means (Table 2) suggest some inaccuracy in the trees per hectare estimates. This is a by-product of applying an ordinary kriging approach, which is essentially a weighted-average interpolation method, to a high-frequency measurement exhibiting considerable variation between neighboring points. Significantly, one would expect similar, but higher, degrees of error with other spatial interpolation methods (e.g., inverse distance-squared weighting), because kriging is typically the best unbiased predictor among conventional interpolation methods (Cressie 1993, Environmental Systems Research Institute 2003). For this analysis, some error in the kriging estimates for individual cells in our host maps is not problematic, because our primary goal was to create maps with simple, effectively ordinal rankings (i.e., from none to very high) of average host density over relatively large areas; indeed, this is why we used a sizeable neighborhood of points (typically 30) during interpolation procedures.

A key observation from the redbay density map is that the *X. glabratus* invasion has thus far developed across a region of South Carolina, Georgia, and northern Florida containing numerous hotspots of moderate to high density. In addition, two hotspots of moderate to high density, one in Georgia and one in South Carolina, fall just beyond the approximate invasion front for *X. glabratus*. In the short term, high redbay levels in these hotspots may promote the rapid expansion of the beetle both northward and westward. Regarding long-term prospects, redbay is mostly found at low densities outside of the above-described areas. This could slow the expansion of *X. glabratus* somewhat, but given the possibility of long-distance dispersal, is unlikely to halt the beetle's advance. With respect to sassafras density, the areas where the species is abundant are far north of the current infestation front. However, sassafras does occasionally reach far enough into the southeastern U.S. coastal plain to

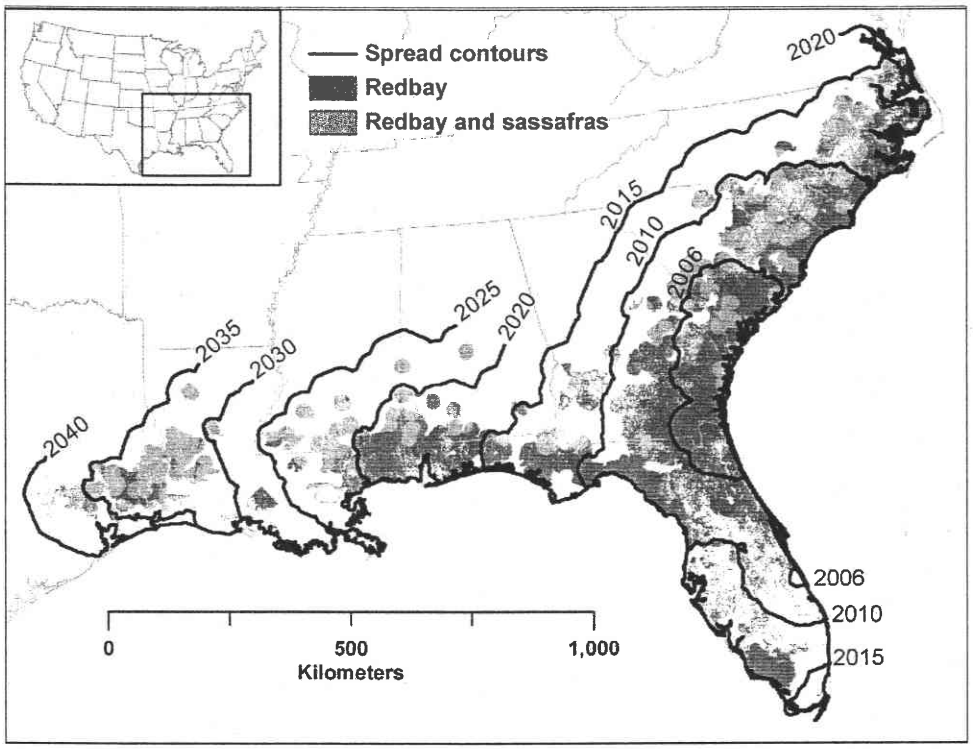

Fig. 6. Predicted extent of *X. glabratus* spread in the eastern United States through time, based on cost-weighted distance modeling from three points of origin, and overlaid on a map of host density.

increase the density of available host in some parts of the coastal region.

Climate Matching. The climate matching tool in NAPPFAST is simple compared with software such as CLIMEX that includes more sophisticated modeling functionality (Vera et al. 2002, Sutherst and Maywald 2005). Nevertheless, the NAPPFAST tool has several advantageous characteristics: an Internet-based interface, a short user learning curve, and a minimal requirement of expert judgment in the modeling process. All climate matching tools are impacted by the quality of the data defining the native distribution of the species of interest. McKenney et al. (2003) noted that a pest species with a restricted extent in its native environment may occupy a very different extent on introduction into a new environment. This observation emphasizes a major criticism of climate matching techniques, that they ignore competition, predation, host interactions, and other factors that serve to constrain a species' distribution to a subset, i.e., its ecological niche, within its full native range (Baker et al. 2000, McKenney et al. 2003, Peterson 2003). These omissions may in turn lead to errors when predicting distribution in other geographic areas. However, climate matching may be the only practical choice given a lack of adequate data to perform other assessments (Baker et al. 2000, Logan et al. 2003). Were they to become available, specific location data on the occurrence of *X. glabratus* within its native range, rather than entire countries or regions, would allow us to refine our estimates of the beetle's extent in the United States, as might any laboratory experiments on critical climatic thresholds for *X. glabratus* or the laurel wilt fungus. We are also currently examining how more detailed location data regarding native host species distributions might help to refine our estimates.

Despite its limitations, our climate match analysis provides evidence that *X. glabratus* may essentially be constrained to the southeastern U.S. coastal plain and is unlikely to spread deep into eastern U.S. interior forests. This departs from historical examples of other Asian xyleborine species that have been present in the United States for at least 15 yr (e.g., *Xyleborus atratus* Eichhoff, *Xylosandrus germanus* Blandford) and that now have broad geographic distributions spanning much of the eastern United States (Rabaglia et al. 2006). A more recently introduced Asian species, *Xylosandrus mutilatus* Blandford, which has so far been found in Mississippi, Florida, and Texas, has also been predicted to eventually extend across much of the eastern United States (Schiefer and Bright 2004, Rabaglia et al. 2006). Nonetheless, it is important to note that all of these species have much broader native geographic ranges than *X. glabratus*, which seems to be limited to subtropical or warm temperate parts of eastern Asia (Holistic Insect Systematics Laboratory 2004, Schiefer and Bright 2004).

The restricted extent predicted for *X. glabratus* principally derives from the minimum monthly rainfall values recorded from the beetle's native range

(Table 1). Particularly during late summer months, most of the conterminous United States receives less rainfall than the smallest amount of rainfall recorded in any part of the native range of *X. glabratus*. This is critical because fungal symbionts of ambrosia beetles generally have exacting moisture requirements: If there is too much moisture, adult beetles and larvae will drown in an overabundance of fungi, whereas too little moisture will kill the fungi, leaving no food source (Furniss and Carolin 1977). No part of the conterminous United States receives monthly rainfall amounts close to the maximum values recorded from the beetle's native range in Asia, so an overabundance of fungus seems unlikely. However, a case can be made that only the southeastern U.S. coastal plain has sufficient rainfall across the months of the growing season to sustain the beetle's fungal symbiont.

Spread Modeling. Our cost-based modeling approach allowed us to make reasonable spread projections despite scant information regarding the population dynamics of *X. glabratus* or its associated fungus. It is also a departure from most invasion models that assume resource (e.g., host) availability does not affect dispersal (Dwyer and Morris 2006). Our approach does have a few shortcomings. First, our assumption of simple radial diffusion does not address possible host-independent variability in rates of spread between different areas. For example, with respect to the initial infestation zone near the Georgia-South Carolina border, it appears from Fig. 1 that *X. glabratus* has spread more rapidly into northern Georgia than into southern South Carolina, despite similar levels of redbay in both areas. Although southern Georgia may have been impacted by dispersal of *X. glabratus* from recent infestations in Florida, this seems an inadequate explanation of the beetle's rapid spread in northern Georgia during the past few years. Actually, the discrepancy between Georgia and South Carolina may be somewhat artificial, because *X. glabratus* invasion is recent (i.e., only limited data available), and there may be a time lag between when a county is actually infested and when infestation is detected and confirmed, not to mention that this discrepancy was observed from coarse, county-level infestation data. Beyond our limiting assumption of radial diffusion, because our approach does not include population parameters, we are unable to model Allee effects or other population-related phenomena that alter the speed of invasions through both space and time (Tobin et al. 2007b). Our model also does not account for certain anthropogenic effects that can change the course of an invasion through time (Liebhold et al. 1992), most obviously the possibility of accidental long-distance dispersal, which has almost certainly occurred with *X. glabratus*. In view of this particular limitation, our model should be seen as the most current estimate of the main front of the *X. glabratus* invasion, while recognizing that isolated infestations may exist, undetected, in locations beyond this main front. Incorporating a means to predict long-distance dispersal events in our model would make it more realistic, as would including population parameters, both of which we hope to do as additional data on the pest's biology and behavior become available.

It is also worth noting that we estimated the mean rate of spread for *X. glabratus* from just the first 3 yr of infestation data. Although the 2007 data were incomplete at the time of our analysis, it initially seems that fewer counties were infested in 2007 than in each of the 3 previous yr. This may indicate that the rate of spread is declining through time, emphasizing that our spread prediction should only be interpreted as preliminary and subject to change as we incorporate additional data.

Evaluating the Overall Threat. Potential ecological and economic impacts are pertinent to assessment of the risk *X. glabratus* poses to the eastern United States. The susceptibility of two endangered shrubs, pondberry and pondspice, to the laurel wilt fungus has already been noted. Neither redbay or sassafras is typically a forest dominant, although redbay is quite common in barrier island forests of the southeastern United States, where it can be one of the most densely growing understory species (Helm et al. 1991). Redbay and sassafras are important food sources for wildlife, particularly in providing winter forage (Griggs 1990, Coder 2006a). Two butterflies, the spicebush swallowtail (*Papilio troilus* L.) and the Palamedes swallowtail (*P. palamedes* Drury), use Lauraceae species as hosts. Although *P. palamedes* larvae may feed on redbay or sassafras, adult females strongly prefer to oviposit on redbay, perhaps because of greater predation pressure on sassafras (Lederhouse et al. 1992). A removal of their preferred host could be catastrophic because, in addition to this possible predation pressure, sassafras density may be inadequate to support populations of *P. palamedes* in their current range.

Because neither redbay nor sassafras is commercially significant, the greatest potential economic impact may come if *X. glabratus* invades the avocado-growing region of south Florida. Although limited in scope (2,935 ha in cultivation), the Florida avocado industry is relatively lucrative; the 2004–2005 harvest had an estimated value of $14.45 million (Evans and Nalampang 2006). Nearly 99% of the state's avocado orchards are found in the Miami-Dade County area (USDA National Agricultural Statistics Service 2004). Our spread model projects that *X. glabratus* could reach this area by 2018, but the actual impact of the beetle's arrival is uncertain, because there is laboratory evidence that avocado may be more resistant to the laurel wilt fungus than other potential hosts (USDA Forest Service 2007b).

What are the prospects for minimizing these impacts? Our analysis suggests that *X. glabratus* and the laurel wilt fungus could expand throughout the southeastern U.S. coastal plain with particular speed during the next several years as host density remains high. The climate match map (Fig. 4) does seem to suggest that the far western extent of redbay is not particularly suitable for the beetle, but this interpretation should be viewed circumspectly given the rudimentary nature of the climate match analysis. It is possible that *X. glabratus* will expand into interior forests of the east-

ern United States, but this seems unlikely given the lack of evidence that the beetle will infest sassafras in the absence of redbay, as well as the apparent climatic constraints. With respect to management, fungicide trials to protect individual trees are ongoing (USDA Forest Service 2007b), but chemical control is probably impractical for natural forest stands. Little prior research exists regarding biological control of xyleborine species (Rabaglia 2003), so whereas that may be an eventual possibility, it is doubtful that a systematic control program could be in place before *X. glabratus* spreads to much of the range of redbay or to the avocado-growing region of Florida unless the beetle's spread is slowed significantly. Development of resistant hosts can be expected to have a similarly long timeframe. Sanitation (i.e., removal of infected hosts) could help to slow the spread of *X. glabratus*—and grant more time to research these other options—if targeted and timed appropriately (USDA Forest Service 2007b). Our analysis offers a basic framework for monitoring *X. glabratus* and planning such sanitation procedures. Ultimately, a key method to slow the spread of *X. glabratus* is to disrupt accidental anthropogenic dispersal, which seems to have moved the beetle long distances on at least a couple of occasions (USDA Forest Service 2007b). Efforts to promote public awareness, when coupled with research and technology transfer, have helped to slow the spread of some forest insect pests in the past (Hain 2006), so pest alerts and outreach publications for *X. glabratus* (Coder 2006b, Mayfield and Thomas 2006) are important in this regard. As a complement, data from our analysis could be used in conjunction with additional GIS data (e.g., on transportation networks) to target those areas where disruption of human-mediated dispersal pathways would likely be most effective.

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